

TAXONOMY OF THE AUSTRALIAN RAINFOREST SNAIL, *HELIX BELLENDENKERENSIS* BRAZIER, 1875 (MOLLUSCA: EUPULMONATA: CAMAENIDAE)

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The taxonomy of *Helix bellendenkerensis* Brazier, 1875 from the Wet Tropics Biogeographic Region, northeastern Queensland is reviewed. Reproductive anatomy and shell micro-sculpture were examined and indicate that this species is not closely related to other species grouped in *Hadra* Albers, 1860 (type: *Helix bipartita* Ferussac, 1822) by Smith (1992). Consequently *Gnarosophia* Iredale, 1933 with *H. bellendenkerensis* as type, is removed from the synonymy of *Hadra* and re-established as a monotypic genus. *Helix heddoniae* Brazier, 1878, *Thersites castanea* Odhner, 1917, *Gnarosophia humoricola* Iredale, 1937 and *Thersites pterinus* Clench and Archer, 1938 are considered to be synonyms of *H. bellendenkerensis*. Details of the habitat and distribution of *H. bellendenkerensis* are provided and it is concluded that this species was most likely an early coloniser of the base-of-the-cape rainforests. Records indicate that it is altitudinally restricted to rainforest above 400m where microclimates are wetter than in the lowlands. Its present distribution within the Wet Tropics is considered to be the result of fragmentation and contraction of rainforest resulting from mid- to late Tertiary climatic changes. □ *Australia, rainforest, taxonomy, Mollusca, Camaenidae, Gnarosophia*

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One of the most speciose groups of land snails in Australia is the Camaenidae. It is common in many parts of the continent but has radiated prolifically in the rainforests of eastern Australia (Solem, 1992, 1998). Representatives of the family occur from the islands of the Torres Strait to Victoria but diversity attenuates from north to south with relatively few occurring south of the Sydney Basin, central New South Wales. Its origins are considered to be in the land masses north of Australia with initial immigration occurring after the collision of the Asian and Australian plates (McMichael & Iredale, 1959; Bishop, 1981; Smith & Stanisic, 1998; Solem, 1992, 1998).

Shell form among the eastern Australian camaenids is diverse and a number of subgroupings (including both genera and nominal families) have been proposed on the basis of gross similarity in shell characters (Iredale, 1933, 1937, 1938). Among these is a group of mainly Queensland camaenids that inhabit rainforest and whose members are characterised by large and often banded shells. These species have been loosely referred to as the 'hadroid' camaenids, a term stemming from their placement in the section *Hadra* of the conglomerate genus *Helix* by Pilsbry (1890). They have been the focus of

shell collectors over many years but their current classification is severely flawed and in need of review.

One of the major stumbling blocks to such a revision is the confusion surrounding existing names. Many taxa (species and genera) have been established based on broad shell characters (size, shape and colour) (Iredale, 1933, 1937, 1938). Investigations have shown that these shell characters may be influenced by local factors (environmental selection) and can be highly convergent in distantly related species. This has also been demonstrated in Western Australian Camaenidae by Solem (1985). Many of the Iredalean taxa been criticised for their poor scientific basis (Solem, 1959; Zilch, 1959; Burch, 1976) and need to be reassessed. But Iredale (1937) did stress that his arrangement was 'purely tentative' and intended merely to create minimal order from the existing chaos.

Few details are available on the anatomy of the hadroids. Hedley (1890), Pilsbry (1894), Bishop (1978a, b), Solem (1979, 1992) and Stanisic (1996a, b) represent the bare handful of articles that have attempted to provide some information on the reproductive anatomy of the hadroids. These studies, particularly the pioneering work of Pilsbry (1894), indicate that a comprehensive

study of their genitalia would lead to a more stable arrangement of taxa than is currently the case.

The proliferation of species-level taxa among the hadroid camaenids in the past has also been exacerbated by brief descriptions, lack of accompanying illustrations and limited access to existing type material. Hence most type material of these species needs re-examination prior to dealing with the many undescribed hadroid species now known from Queensland (Stanisic, unpubl.). Typical of this confusion is the case recently outlined by Stanisic (1998) for *Temporena whartoni* (Cox, 1871) from the Bowen area, northeastern Queensland.

At least 45 camaenids occur in the Wet Tropics Biogeographic Region of northeastern Queensland, many undescribed (Stanisic et al., 1994). These include a number of hadroids with diverse shell form that inhabit rainforest habitats ranging from humid lowland rainforest to dry vine thickets. This study examines key aspects of the morphology of *Helix bellendenkerensis* Brazier, 1875, a species occurring mainly in the upland and highland rainforests of the Wet Tropics. It is currently associated with the large camaenids belonging to *Hadra* Albers, 1860 (Smith, 1992). Herein, the reproductive anatomy and shell microsculpture of *Helix bellendenkerensis* are analysed and compared with patterns found in *Hadra* spp.

All material used in this study is in the Queensland Museum, Brisbane (QMMO) and the Australian Museum, Sydney (AMSC), Australia. One listed specimen is from the Naturhistoriske Riksmuseum, Stockholm, Sweden (NHRM1545). This specimen was not sighted and the citation is based on Smith (1992).

Abbreviations used in the specimen list are as follows. Collectors: DC, D.J. Cook; DP, D. Potter; DY, D.K. Yeates; GM, G.B. Monteith; GT, G. Thompson; HJ, H.A. Janetzki; HD, H. Dick; IF, I. Fanning; IL, I. Loch; JC, J. Covacevich; JS, J. Stanisic; KM, K. McDonald; LR, L. Roberts; MB, M.J. Bishop; RL, R. Leggett; RS, R. Sheridan; SJ, S.W. Jackson; SW, S. Wilson. Others: Exped, Expedition; EW, Earthwatch; L, Lake; NP, National Park; NVF, notophyll vine forest; SF, State Forest; SMVFT, simple microphyll vine-fern thicket; Tbl, Tableland; Ra, Range; R, River.

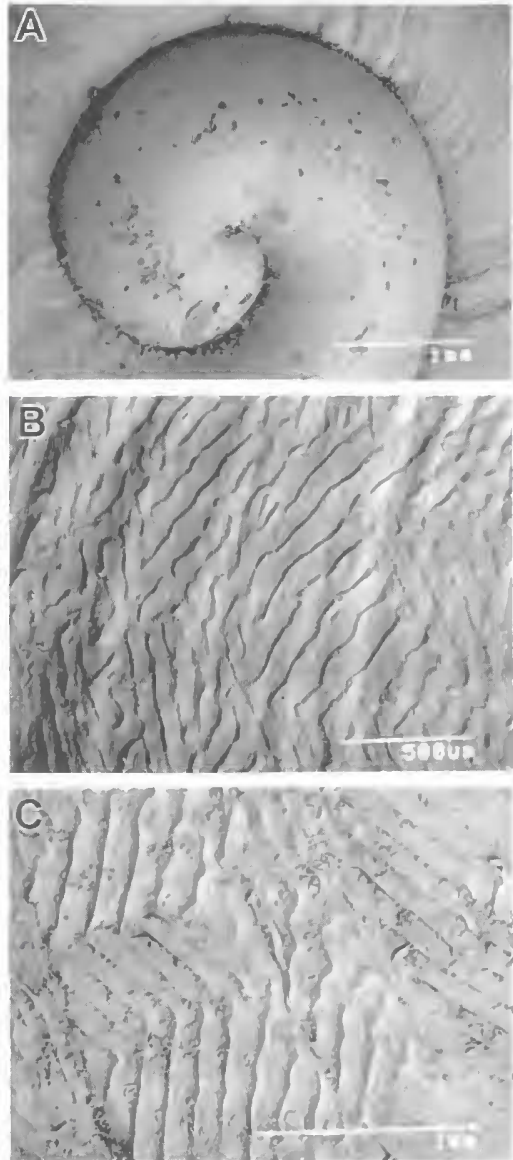


FIG. 1. *Gnarosophia bellendenkerensis*, QM MO48283. A, protoconch; B, sculpture on early adult whorls; C, sculpture on body whorl. Scale lines as marked.

PREVIOUS STUDIES

Pilsbry (1890) first placed *Helix bellendenkerensis* Brazier, 1875 in the sub-grouping *Hadra* Albers, 1860 (type *Hadra bipartita* Ferussac,

1822) within *Helix*. Subsequently Pilsbry (1894) made *Hadra* a section of the subgenus *Thersites* Pfeiffer, 1855 (type: *Helix richmondiana* Reeve, 1852 and moved *H. bellendenkerensis* to the section *Sphaerospira* Mörch, 1867 (type: *Helix fraseri* Griffith & Pidgeon, 1833) within *Thersites*. Most of the eastern Queensland camaenids with large and striped shells were included here. Pilsbry's studies were based on both shell characters and reproductive anatomy, and while incomplete, were beginning to resolve a very confused situation. However, as Fulton (1904) pointed out, the lack of 'authentic' material made his task difficult. Fulton (1904), armed with types, co-types and the knowledge gained from studying a number of local collections, including that of Dr J.C. Cox (author of the first monograph of Australian land shells and many of the early hadroid species), revised Pilsbry's section *Sphaerospira*. Consequently several species were excluded, including *Helix bellendenkerensis* which was tentatively placed in *Hadra*. Iredale (1933) considered this species to differ significantly from *Hadra* because of its 'strong wrinkled sculpture' and introduced *Gnarosophia* to accommodate it (as type), and a number of other northeastern Queensland camaenids. This classification was maintained by Iredale (1937) in his list of the Australian land Mollusca. Smith (1992) synonymised *Gnarosophia* and the far north Queensland *Micardista* Iredale 1933 (type: *Helix (Camaena) barneyi* Cox, 1873) with *Hadra*. Smith (1992) incorporated nine species in *Hadra*: *H. bipartita*, *H. barneyi*, *H. webbi* (Pilsbry, 1900), *H. bartschi* (Marshall, 1927), *H. funiculata* (Reeve, 1854), *H. semicastanea* (Pfeiffer, 1859), *H. wilsoni* (Solem, 1979), *H. beddomae* (Brazier, 1878) and *H. bellendenkerensis*.

THIS STUDY

Scanning electron microscopy revealed that the wrinkled periostracal sculpture of *Helix bellendenkerensis* consists of radially disposed ridges occasionally arranged in a chevron-like pattern (Fig. 1B,C) that extend from the first post-embryonic whorls to the body whorl. These are also present in *H. beddomae* but are absent in *H. bipartita*, *H. barneyi*, *H. webbi*, *H. funiculata*, *H. semicastanea* and *H. bartschi* in which the early adult whorls display a pattern of crowded to scattered pustules that on later whorls give rise to a series of pustules and ridgelets arranged in vaguely spiral rows. This basic structural difference in microsculpture suggests that *H.*

bellendenkerensis and *H. beddomae* are not closely related to the main mass of *Hadra* spp. *H. wilsoni* was not examined.

The reproductive anatomy of *H. bipartita* was detailed by Solem (1979) and showed several important features which this species has in common with *H. webbi*, *H. barneyi*, *Jacksonena rudis* (Hedley, 1912) and species grouped in *Spurlingia* Iredale, 1933 by Smith (1992) (Stanisic, unpubl.). The penis in these species is short, tubular and lacks a verge. The penial chamber has a series of longitudinal thickenings that may be supplemented by a short pustular zone apically. An apical collar separates the penis from the epiphallus. Epiphallic caeca (one on the epiphallus and one at the epiphallus-vas deferens junction) are also present. *S. forsteriana* (formerly placed in *Zyghelix* Iredale, 1933) shows some deviation from this general pattern in having the male genitalia very elongated, but otherwise has the characters that align it with the *Hadra-Spurlingia-Jacksonena* lineage. Detailed data on these species will be presented elsewhere but the important point is that they form a strongly cohesive unit based on their reproductive anatomy. Significantly though, this anatomical cohesion belies gross differences in shell morphology of genera within this lineage. In contrast the reproductive structures of *Helix bellendenkerensis* show several significant departures from these species. The penis is very elongate with a sculptured cylindrical verge through which the epiphallus opens (Fig. 2B). The upper third of the penial chamber has crowded, sub-rectangular pustules while thick fleshy longitudinal ridges are present in the lower two thirds. There is no apical penial collar; a knob-like epiphallic caecum is present at about halfway along its length; and a long, tapering, muscular flagellum emanates from the epiphallus-vas deferens junction (Fig. 2A). These differences separate *H. bellendenkerensis* from the *Hadra-Spurlingia-Jacksonena* lineage and indicate that this species deserves separate generic status. Although *H. beddomae* was not dissected, the shell microsculpture aligns this species with *Helix bellendenkerensis*. It is herein considered a synonym of that species pending the examination of the reproductive anatomy. A revised taxonomy including a redescription of *Helix bellendenkerensis* is presented below.

Order EUPULMONATA
Superfamily CAMAENOIDEA
Family CAMAENIDAE

Gnarosophia Iredale, 1933

Gnarosophia Iredale, 1933: 46; Iredale, 1937: 25; Burch, 1976: 135; Smith, 1992: 129 (in synonymy).

TYPE SPECIES. *Helix bellendenkerensis* Brazier, 1875-by original designation.

DIAGNOSIS. Shell large to very large with microsculpture of crowded, radially disposed microridgelets occasionally arranged in a chevron-like pattern. Protoconch and first teleoconch whorl with vague radial growth lines, tending to be smooth. Penial chamber with crowded sub-rectangular to rhomboidal pustules apically; longitudinal ridges basally. Epiphallus relatively short (less than half length of penis), opening into penis through prominent sculptured, cylindrical verge; knob-like epiphallic caecum about halfway along length of epiphallus and a long, tapering epiphallic flagellum present at the epiphallus-vas deferens junction.

REMARKS. *Gnarosophia* is herein considered to be a monotypic genus. The status of other species placed in *Gnarosophia* by Iredale (1937) is not reviewed here. These species have a superficially similar periostracal microsculpture to *Gnarosophia bellendenkerensis* but differ significantly from this species in reproductive anatomy (Stanisic, unpubl.). Closer examination of the periostracal microsculpture of these species also reveals important differences in the structure and disposition of the micro-ridges compared with *G. bellendenkerensis*. They appear to form a monophyletic assemblage but are not considered to be closely related to *H. bellendenkerensis*.

Gnarosophia bellendenkerensis Brazier, 1875
(Figs 1-4)

Helix bellendenkerensis Brazier, 1875: 32.

Helix beddomae Brazier, 1878: 80.

Helix (Hadra) bellendenkerensis: Pilsbry, 1890: 161.

Helix (Hadra) beddomae: Pilsbry, 1890: 174.

Thersites (Sphaerospira) bellendenkerensis: Pilsbry, 1894: 134; Cox, 1909: 11.

Thersites (Sphaerospira) beddomae: Pilsbry, 1894: 134; Cox, 1909: 10.

Hadra bellendenkerensis: Fulton, 1904: 10; Smith, 1992

Hadra beddomae: Fulton, 1904: 10; Smith, 1992: 130.

Thersites castanea Odhner, 1917: 87: 123; Smith, 1992: 130 (in synonymy).

Gnarosophia castanea: Iredale, 1937: 26.

Gnarosophia beddomae: Iredale, 1937: 25.

Gnarosophia bellendenkerensis: Iredale 1933: 46; Iredale, 1937: 25.

Gnarosophia humoricola Iredale 1937; Smith, 1992: 130 (in synonymy).

Thersites pterinus Clench & Archer, 1938: 21; Iredale, 1938:123; Smith, 1992: 130 (in synonymy).

COMPARATIVE REMARKS. *Gnarosophia bellendenkerensis* can be distinguished from other large camaenids in the Wet Tropics on the basis of microsculpture, and with rare exception, shell colour. The chevron-like pattern of periostracal wrinkles of *G. bellendenkerensis* is not seen in other Wet Tropics hadroids. *Monteithosites helicostracum* Stanisic, 1996 from Bakers Blue Mt and Hanns Tbl. has spiral wrinkles and *Hadra bipartita* and *H. webbi* have pustules apically and ridgelets toward the aperture. Other Wet Tropics hadroids grouped in *Gnarosophia* by Iredale (1937): *palmensis* Brazier, 1876; *mazei* Brazier, 1878; *bellaria* Iredale, 1937; *rawnsleyi* Cox, 1873; *mourilyani* Brazier, 1875 have pustules on the early spire giving way to radially disposed wrinkles and ridgelets on the latter whorls. These five species have multi-banded shells as does *M. helicostracum*. In contrast, the shell of *G. bellendenkerensis* is brown to black all-over with two light coloured bands only: one subsuturally and one at the periphery. *Hadra bipartita* and *H. webbi* have bi-coloured shells with the apex and spire generally yellow and the base brown to black (rarely yellow all-over). This bipartite colour form is found only in *G. bellendenkerensis* occurring in the Cardwell Ra. No *Hadra* s.s. species are known to occur at this locality.

TYPE MATERIAL. NEQ: HOLOTYPE: AMSC17631, Mt Bellenden Ker, c. 40km S of Cairns, Dalrymple NE Coast Exploring Exped., W. Hill, R. Johnstone, ex. J. Brazier coll (Height of shell = 40.46mm, diameter = 45.46mm, H/D = 0.89, whorls = 6 1/4). OTHER TYPE MATERIAL. AMSC17632, Cardwell Ra., c. 32km NW Cardwell, 1070m, C.E. Beddome, c.1871 (holotype of *Helix beddomae*) (Height of shell = 37.89mm, diameter = 47.19mm, H/D = 0.80, whorls = 6 1/8); AMSC41901, NHRM1545, Cedar Creek, Atherton Tbl., Dr. E.J. Mjoberg, ex. N. Odhner (2 syntypes of *Thersites castanea*) (Height of shell of AMS specimen = 32.07mm, diameter = 38.33mm, H/D = 0.84, whorls = 6 1/8); QMMO1769, L. Barrine, Atherton Tbl., Harvard-Australian Exped., 1932 (holotype of *Thersites pterinus*) (Height of shell = 28.92mm, diameter = 39.08mm, H/D = 0.74, whorls = 5 3/4); AMSC100630, Innisfail, under logs in dense scrub, SJ, 1908 (holotype of *Gnarosophia humoricola*). (Height of shell = 42.86mm, diameter = 52.23mm, H/D = 0.81, whorls = 6 1/8); AMSC106798, 3 adults same data as previous, (paratypes of *G. humoricola*).

OTHER MATERIAL. NEQ: QMMO48769, 1, 12 Mile Scrub, Helenvale (15°46'S, 145°15'E), 300m, Rf., under

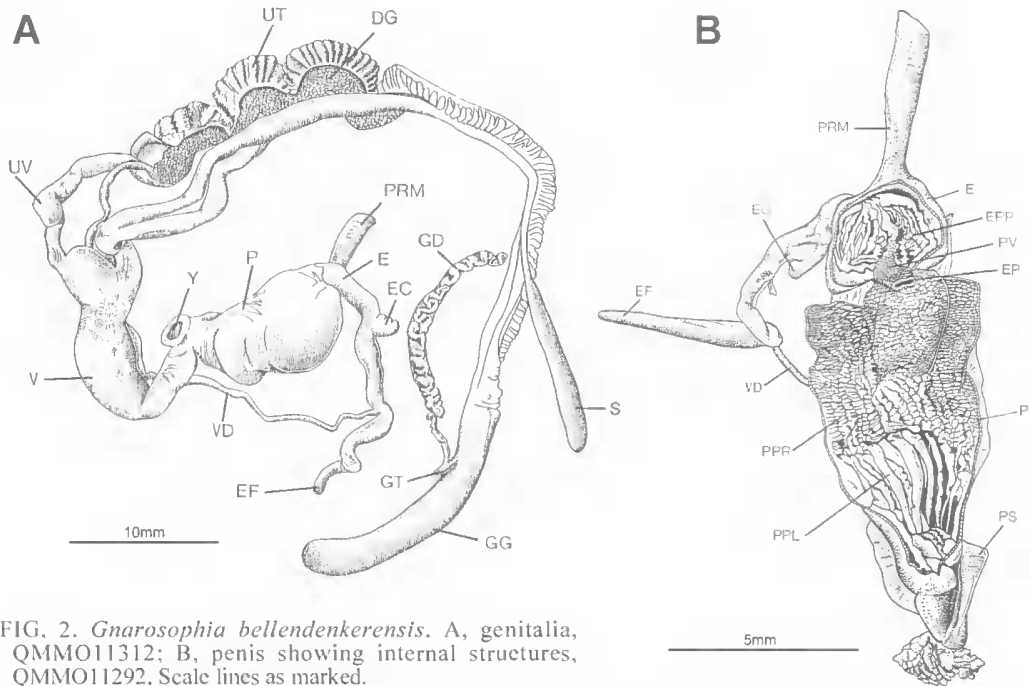


FIG. 2. *Gnarosophia bellendenkerensis*. A, genitalia, QMMO11312; B, penis showing internal structures, QMMO11292. Scale lines as marked.

log. P. Filewood; QMMO56777, 1, summit Mt Hartley S of Helenvale (15°46'S, 145°20'E), 790m, Rf., GM, 8.xi.1995; QMMO48733, 1, summit Mt Finnigan S of Helenvale (15°48'S, 145°17'E), 1050m, Rf., GM, RS, LR, GT, 3.xii.1990; QMMO48555, 1, Mt Sampson S of Helenvale (15°48'S, 145°12'E), 600-790m, Rf., ANZSES Exped., 26.xii.1990; QMMO16426, 2, summit Mt Finnigan S of Helenvale (15°49'S, 145°16'E), 1100m, GM, 29.xi.1985; QMMO48595, 1, Mt Misery S of Helenvale (15°53'S, 145°13'E), 500-850m, Rf., ANZSES Exped., 2.i.1991; QMMO56180, 5, c. 30km SSW Helenvale at Mt Boolbun (15°56'S, 145°08'E), 850m, simple NVF, HJ, GM, JC, 5.xi.1995; CAPE TRIBULATION: QMMO60878, 1, Mt Donovan (16°01'S, 145°25'E), 600m, HD; QMMO48602, 1, Mt Halcyon (16°03'S, 145°25'E), 870m, Rf.,GM, HJ, DC, LR, 22.xi.1993; QMMO48683, 2, Mt Haleyon (16°03'S, 145°25'E), 850m, Rf.,GM, HJ, DC, LR, 22.xi.1993; QMMO48549, 5, 4.5-5.0km W, (16°04'S, 145°25'E), 760-780m, Rf., GM, DY, 21.iv.1983; QMMO47698, 2, Pilgrim Sands (16°04'S, 145°28'E), 20m, Qld Naturalists; QMMO48657, 6, Roaring Meg Valley (16°04'S, 145°25'E), 720m, Rf., GM, HJ, DC, LR, 21.xi.1993; QMMO48578, 1, Mt Pieter Botte (16°05'S, 145°24'E), 950m, Rf., GM, HJ, DC, LR, 21.xi.1993; QMMO60879, 1, Mt Pieter Botte (16°05'S, 145°24'E), 950m, HD; QMMO48764, 1, Mt Sorrow (16°05'S, 145°26'E), 800m, Rf., GM, 19.x.1980; QMMO48633, 2, Mt Hemmant, 6km SW (16°07'S, 145°25'E), 1050m, Rf., GM, HJ, DC, LR, 25.xi.1993; QMMO48696, 1, Mt

Hemmant, 6km SW (16°07'S, 145°25'E), 1050m, Rf.,DC, HJ, LR, 25.xi.1993. THORNTON PEAK: QMMO15049, 1 (16°09'S, 145°21'E), 600m, JC, SW, 22.ix.1984; QMMO48704, 2 (16°10'S, 145°22'E), 1100-1300m, Rf., GM, 24.ix.1984; QMMO48712, 3, (16°10'S, 145°22'E), 1000-1300m, Rf.,GM, DC, 20.ix.1981; QMMO48723, 2, (16°10'S, 145°22'E), 1100-1200m, Rf.,GM, DY, GT, 30 Oct 1983; QMMO48655, 2, Hilda Creek (16°10'S, 145°22'E), 800-900m, Rf.,GM, RL, 25.ix.1984. QMMO59136, 1, Blue Hole, c.10km NE Daintree (16°11'S, 145°24'E), 140m, Rf., under log, JS, 25.ix.1996; QMMO60880, 1, Windsor Tbl. (16°15'S, 145°02'E), 1200m, HD; QMMO48517, 2, Windsor Tbl., 35km NNW Mt Carbine, (16°15'S, 145°02'E), 1150m, Rf.,GM, DY, DC, 25.iv.1982; QMMO10011, 1, Windsor Tbl. (16°17'S, 145°04'E), 850m, edge of Rf., 1F, 30.xii.1980; QMMO10012, 1, Windsor Tbl. (16°17'S, 145°04'E), 850m, edge of Rf., 1F, 29.xii.1980; QMMO48508, 1, Windsor Tbl., 28km NNW Mt Carbine (16°17'S, 145°04'E), 900m, Rf.,GM, DY, DC, 15.iv.1982; QMMO48744, 3, 7km N Mt Spurgeon (16°22'S, 145°13'E), 1250m, Rf., GM, HJ, DC, LR, 17.x.1991; QMMO48330, 2, Black Mt, c.4.5km N Mt Spurgeon (16°24'S, 145°12'E), 1250-1330m, Rf.,GM, HJ, DC, LR, 17.x.1991; QMMO48270, 1, Mossman, 10km NW, Devils Thumb (16°24'S, 145°17'E), 1200m, Rf., GM& RS, 27.xi.1990; QMMO48266, 3, Mossman, 11km NW (16°24'S, 145°16'E), 1330m, Rf., GM, GT, DC, RS, HJ, 27.xi.1990; QMMO48350, 5, Stewart Ck, c.4km NNE Mt

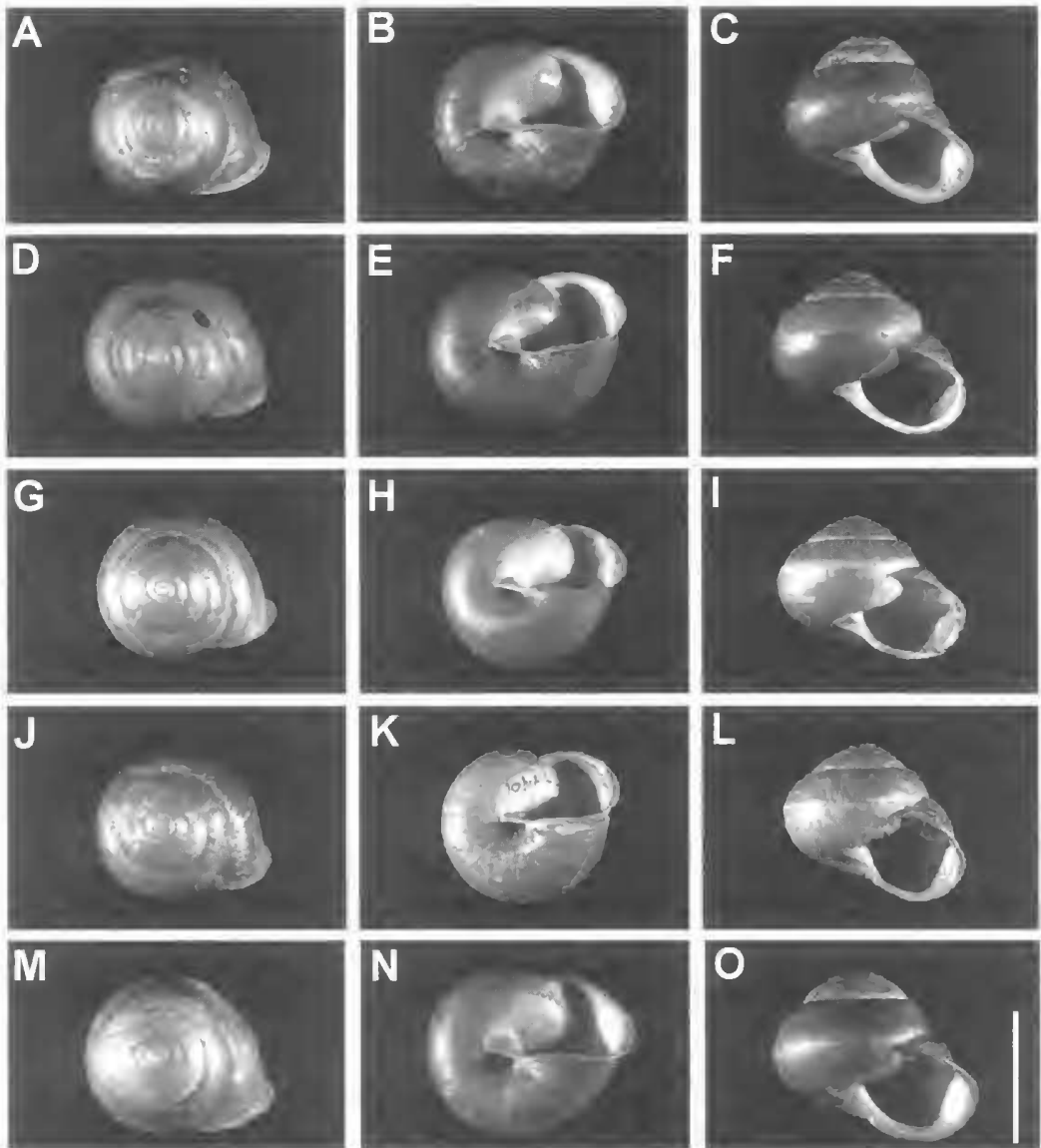


FIG. 3. A-C, AMSC17631, holotype of *Helix bellendenkerensis*; D-F, AMSC17632, holotype of *Helix beddomae*; G-I, QMMO1769, holotype of *Thersites pterinus*; J-L, AMSC41901, syntype of *Thersites castanea*; M-O, AMSC100630, holotype of *Gnarosophia humoricola*. Scale line = 50mm.

Spurgeon (16°24'S, 145°13'E), 1250-1300m, Rf., GM, GT, HJ, DC, LR, 15.x.1991; QMMO48258, 2, Mossman, 12km NW, Roots Ck (16°25'S, 145°16'E), 1200m, Rf., ANZSES Exped., 28.xii.1990; QMMO48283, 2, ANZSES Exped., 1.i.1990, QMMO48287, 1, GM, GT, DC, RS, HJ, 28 Nov 1990, Mossman, 13km W, Pauls Luck (16°26'S, 145°15'E), 1100m, Rf.; QMMO48339, 2, Mt Spurgeon, c.2km SE.

(16°27'S, 145°12'E), 1100m, Rf., GM, HJ, DC, 13.xi.1991; QMMO48299, 4, QMMO48307, 2, GM, GT, 17.xii.1988, QMMO48321, 4, GM, GT, ANZSES, 20.xii.1989, Mossman 9km W, Mossman Bluff Track (16°28'S, 145°17'E), 1000m, Rf.; QMMO31064, 1, Mossman, c.4.4km W, Mossman Gorge (16°29'S, 145°20'E), 200m, Rf., crawling on rock, JS, DP, 29.vi.1983; QMMO48246, 1,

- Mossman, 7km SE, Mt Demi (16°30'S, 145°19'E), 1100m, Rf., DY, GT, 29.x.1983; QMMO16258, 1, JS, 1.x.1980, QMMO48239, 1, ANZSES Exped., 13.i.1990, Mt Lewis Rd, Old Barracks area (16°35'S, 145°16'E), 100m, Rf.; QMMO60242, 2, Mt Lewis, c.6km WNW Julatten (16°35'S, 145°17'E), Rf., under logs, R. Crookshanks, 2.iii.1997; QMMO31054, 2, under logs and rocks, 27.vi.1983, QMMO24605, 2, under logs, 8.x.1988, Mt Lewis (16°36'S, 145°16'E), 1000m, JS, DP; QMMO48209, 3, Julatten, 17km ESE, Black Mt (16°39'S, 145°29'E), 1000m, Rf., GM, DC, DY, 14.iv.1982; QMMO48623, 2, Lamb Ra., Mt Williams (16°55'S, 145°40'E), 1000m, Rf., GM, HJ, DC, 2.xii.1993; QMMO48190, 1, Lamb Ra., Chujeba Peak summit (16°56'S, 145°39'E), 1000m, Rf., GM, GT, 14.xii.1989; QMMO48439, 1, Lamb Ra., 20km SE Mareeba, Davies Ck Rd (17°02'S, 145°35'E), 750m, Rf., GM, GT, 17.xii.1989; QMMO48193, 4, GM, GT, QMMO48206, 1, GM, GT, HJ, Lambs Head, 10km W Edmonton (17°02'S, 145°38'E), 1200m, Rf.; QMMO24797, 2, Lamb Ra., c.17.5km along Davies Ck Rd from Cairns-Mareeba Rd (17°03'S, 145°37'E), 1000m, Rf., under log, JS, DP, 11.x.1988; QMMO48582, 4, QMMO48663, 1, Lambs Head, E, Isley Hills (17°03'S, 145°42'E), 1050m, Rf., GM, HJ, DC, 30.xi.1993; QMMO48692, 1, Lambs Head, NW, upper Isley Ck (17°03'S, 145°41'E), 750m, Rf., GM, HJ, DC, 29.xi.1993; QMMO48139, 1, Malbon Thompson Ra., North Bell Peak (17°05'S, 145°53'E), 900-1000m, Rf., GM, DC, 15.ix.1981; QMMO48156, 2, Lamb Ra., Mt Edith (17°06'S, 145°37'E), 1000m, Rf., GM, DY, GT, 12.x.1982; QMMO25925, 1, Lamb Ra., c.1.9km N Tinaroo SF Rd, Tinaroo Dam- Mt Edith Rd (17°07'S, 145°37'E), 700m, Rf., under log, JS, DP, 12.x.1988; QMMO25927, 1, Lamb Ra., c.0.9km N Tinaroo SF Rd, Tinaroo Dam- Mt Edith Rd (17°08'S, 145°37'E), 700m, Rf., under log, JS, DP, 12 Jct 1988; QMMO60241, 2, Cairns, S, lower Mulgrave R. (17°11'S, 145°54'E), Rf., under logs, R. Crookshanks, 25.ii.1997; QMMO6903, 1, Atherton Tbl., L. Barrine (17°15'S, 145°36'E), 800m, MB; QMMO1769, 1, Atherton Tbl., L. Barrine (17°15'S, 145°38'E), Harvard Exped., 1931-32. MT BELLENDEN KER: QMMO48765, 1, 25.x.1981, QMMO11252, 1, 17.x.1981, summit Centre Peak (17°15'S, 145°51'E), 1560m, SMVFT, EW/QM; QMMO11312, 4, 25.x.1981, QMMO11328, 1, 1.xi.1981, 1km S cable tower 6 (17°16'S, 145°53'E), 500m, Rf., EW/QM; QMMO11361, 3, c.1km N (17°16'S, 145°53'E), 100m, Rf., EW/QM, 1.xi.1981; QMMO11329, 6, 1.xi.1981, QMMO48565, 3, Rf., 25.x.1981, cable tower 3 (17°16'S, 145°52'E), 1054m, EW/QM; QMMO11276, 4, EW/QM, 17.xi.1981, QMMO11292, 6, EW/QM, 25.x.1981, QMMO31235, 1, under log, 3.vii.1983, JS, DP, cableway base (17°16'S, 145°53'E), 100m, rainforest; QMMO31245, 1, just below summit (17°16'S, 145°51'E), 1500m, under logs, JS, DP, 4.vii.1983; QMMO48061, 2, c.4km W centre peak (17°16'S, 145°49'E) 1250m, Rf., GM, HJ, DC, 9.x.1991. QMMO50347, 2, Atherton Tbl., 2km W Yungaburra, Thomas Rd (17°16'S, 145°34'E), Rf., on forest floor and tree bases, 11.v.1996; QMMO6910, 7, Atherton Tbl., L. Eacham (17°17'S, 145°36'E), 800m, MB; QMMO16299, 1, Atherton Tbl., L. Eacham (17°17'S, 145°37'E), 800m, Rf., under log, H. Vokes, 29.ix.1980; QMMO48766, 1, GM, 8.x.1980, QMMO51732, 1, L. Winsor, 15.ix.1977, Atherton Tbl., Malanda Falls (17°21'S, 145°35'E), 750m, Rf., MT BARTLE FRERE: QMMO11415, 1, summit NW peak (17°23'S, 145°48'E), 1440m, SMVFT, EW/QM, 8.xi.1981; QMMO48079, 1, NW to Centre peak (17°23'S, 145°48'E), 1500m, Rf., EW/QM, 7.xi.1981; QMMO11401, 2, summit Centre peak (17°23'S, 145°48'E), 1540m, SMVFT, EW/QM, 7.xi.1981; QMMO11373, 3, walking track below NW peak (17°23'S, 145°48'E), 1540m, SMVFT, EW/QM, 8.xi.1981; QMMO11391, 3, summit S peak (17°24'S, 145°49'E), 1620m, SMVFT, EW/QM, 7.xi.1981; QMMO11372, 2, Centre-S peak, (17°24'S, 145°49'E), 1500m, SMVFT, EW/QM, 8.xi.1981. QMMO9914, 2, R. Raven, 6.iv.1978, QMMO48463, 1, Rf., GM, GT, 8.xii.1988, QMMO48763, 8, Rf., under logs, KM, 1.iv.1978, Atherton Tbl., Boonjie Scrub, ESE Malanda (17°24'S, 145°43'E), 700m; QMMO26082, 2, Mt Hypipamee NP, The Crater, N Ravenshoe (17°25'S, 145°29'E), 950m, Rf., under logs, JS, DP, 13.x.1988; QMMO56596, 2, Mt Hypipamee NP, The Crater, N Ravenshoe (17°25'S, 145°29'E), 980m, KM, 16.iii.1994; QMMO46333, 1, Hugh Nelson Ra., N of Ravenshoe (17°27'S, 145°29'E), 1100m, J. Short, P. Davie, 31.x.1993; QMMO48038, 2, Atherton Tbl., 7km SW Millaa Millaa, Kjellberg Rd (17°33'S, 145°33'E), 1050-1100m, Rf., GM, DC, DY, 27.iv.1982; QMMO16220, 3, Palmerston Hwy, Fishers Ck (17°34'S, 145°53'E), 100m, Rf., litter, JS, 28.ix.1980; QMMO48034, 1, Ravenshoe, NE at Mt Fisher (17°34'S, 145°34'E), 1000-1200m, Rf., GM, DY, 5.v.1983; QMMO6902, 1, Palmerston Hwy (17°35'S, 145°45'E), 500m, MB; QMMO48049, 1, Palmerston NP (17°35'S, 145°42'E), 350-400m, Rf., GM, 2.i.1990; QMMO16229, 1, Palmerston Hwy, Douglas Ck (17°36'S, 145°43'E), 500m, Rf., litter, JS, 28.ix.1980; QMMO48059, 1, Atherton Tbl., 12km SW Millaa Millaa, Massey Ck (17°37'S, 145°33'E), 1000m, Rf., among litter, GM, DY, 4.v.1983; QMMO48412, 1, Atherton Tbl., 25km SE Millaa Millaa, Downcy Ck (17°39'S, 145°46'E), 400m, Rf., GM, GT, 7.xii.1988; QMMO11841, 1, Ravenshoe, 20km S (17°46'S, 145°33'E), 780m, Rf., S van Dyck, K. Plowman; QMMO48002, 2, Tully, 11km N, upper Boulder Ck (17°50'S, 145°54'E), 800m, Rf., GM, GT, HJ, 4.xii.1989; QMMO30449, 1, Tully, Tabletop Ra. (17°53'S, 145°48'E), 80m, C. Welzel; QMMO60895, 2, Tully, 15km NE, along Mission Beach Rd (17°54'S, 146°04'E), 20m, Rf., under logs, R. Crookshanks, L. Free, 12.xii.1997; QMMO20180, 1, Tully, W, Tully R. valley (17°55'S, 145°50'E), 20m, JS, DP, 9.vi.1983; QMMO55680, 3, Tully, E at Mt Mackay (17°57'S, 145°58'E), under logs and rocks, J. Leroi; QMMO17460, 1, Cardwell Ra., slopes of Mt Pershouse (18°14'S, 145°47'E), 1000m, Rf., under log, KM; AMSC5545, 1, 32km NW Cardwell, in ranges at 1050m, ex C. Hedley; AMSC106675, 1 Telegraph Ra., on road to Cashmere via Cardwell; AMSC106755, 3, Kuranda, near Cairns, W. Day; AMSC106752, 2, Mulgrave R., S of

Cairns, Macleay, ex Cox coll; AMSC106754, inland from Cairns, Allen, i.1914; AMSC172709, 1, L. Eacham, Rf., ex. F.E. Allen; AMSC106773, 3, Johnstone R., in dense scrub, SJ, xii.1908; AMSC106763, 3, near Innisfail, ex. C. Horton, xii.1959; AMSC106762, 1, Cairns, back of Carrington, w. Black, ex Cox coll; AMSC106753, 1, Bellenden Ker Ra.: AMSC106756, 1, Tinaroo Scrubs, SW Cairns, SJ, xii.1908; AMSC106758, 1, Wongabel SF., c.8km S Atherton, P. Colman, iii.1959; AMSC106761, 1, Cairns, C.J. Wild; AMSC106760, 1, Atherton, ex. Atherton High School, v.1959; AMSC106757, 6, Tinaroo Scrub, Atherton district, in damp places, SJ, xi.1908; AMSC106795, 2, Mulgrave R., ex Macleay Museum; AMSC76588, 2, Little Mulgrave Scrub, near Gordonvale, G. Coates; AMSC106772, 2, Daintree R., 40km N Mossman, L. Price, x.1958; AMSC106764, 4, Yungaburra, Atherton Tbl., A.J. Marsh; AMSC106797, 1, Mt Alexander, near Mossman; AMSC106796, 1, Babinda area, near Innisfail, A.E. Johnson, 1964; AMSC106774, 14, Mulgrave R., W. Froggatt, ex Macleay Museum; AMSC124130, 3, Coquette Point, Innisfail, B. Collins, 1979; AMSC149360, SF at Greenhaven, Palmerston Hwy, under wood on track in Rf., IL, 9.x.1985; AMSC105538, 5, L. Eacham, 18.ix.1949; AMSC172705, 3, Belson's Scrub, Atherton Tbl., ex F.E. Allen; AMSC127071, 1, Jarrah Creek, at Tully-Cardstone road crossing, W of Tully, in flood debris on creek bank, W.F. Ponder & IL, 27.ix.1980; AMSC125806, 1, Chammillin Creek at Tully Falls, NVF, IL, 28.ix.1980; AMSC117978, 1, Jordan Goldfield, off Palmerston Hwy, near Innisfail, under log, IL, 10.vi.1973; AMSC158708, 1, in garden between Gordonvale and Cairns, 25.iv.1973, ex M. Shea; AMSC168511, 2, W of Cape Tribulation, 740m, granite outcrop in Rf., *Pitta* predation, HD, ix.1991.

DESCRIPTION. Shell large to very large, diameter 33-50mm (mean 40.19mm) with $5\frac{1}{8}+$ - $6\frac{5}{8}$ (mean $5\frac{3}{4}$) normally coiled whorls. Apex and spire moderately to strongly elevated, height 26.10-42.50mm (mean 33.08mm), H/D ratio 0.70-0.94 (mean 0.82). Protoconch of 2 whorls, sculptured with very weak radial growth lines. Post-apical whorls with fine, obliquely to radially disposed, crowded periostracal ridges occasionally arranged in a chevron pattern, not continuous on base. Base rounded with distinct excavation around umbilicus, sculptured with fine radial growth lines. Shell periphery rounded, body whorl inflated, descending rapidly for a short distance behind aperture. Aperture subovate and strongly inclined from shell axis. Umbilicus narrow, more than two-thirds covered by lip. Colour brown to dark brown with two lighter coloured bands, one below the suture and one at the shell periphery; rarely without bands and two toned: dark yellow above and brown to black below the periphery. Lip and behind aperture brown to dark brown. Based on 97 measured adults.

Genitalia (Fig. 2A,B) with hermaphroditic duct (GD) entering talon (GT) laterally; talon head knob-like. Prostate (DG) and uterus (UT) without unusual features. Short, relatively long, free oviduct (UV) and short barrel-shaped vagina (V), internally with longitudinal thickenings. Spermatheca (S) with long stalk and clavate head that reaches the base of a rather elongate albumen gland (GG). Vas deferens (VD) a thin tube, entering epiphallus (E) through a simple pore; a long tapered, muscular epiphallic flagellum (EF) present at junction. Epiphallus relatively short, reflexed with thin muscular ascending arm and shorter thick descending arm; descending portion with short, fleshy, ridge-like pilasters (EPP) internally; knob-like epiphallic caecum (EC) present about halfway along ascending arm. Penial retractor muscle (PRM) inserted apically on descending arm of epiphallus. Epiphallus entering penis through sculptured, cylindrical verge (PV); epiphallic pore (EP) terminal on verge. Penis (P) relatively long (2 times length of vagina), cylindrical, folded within moderately strong sheath (PS). Penial chamber with crowded, diamond-shaped to sub-rectangular pustules (PPR) in top third and fleshy, longitudinal thickenings (PPL) in lower two thirds and continuing into short atrium (Y).

Animal colour grey to dark grey and almost black in parts (Fig. 4). Head wart present. Based on 3 dissected adults, QMMO11292, MO11312.

DISTRIBUTION AND HABITAT. Wet Tropics Biogeographic Region from just south of Cooktown to north-west of Cardwell (Fig. 5); under logs in rainforest usually above 400m.

REMARKS. The shell of *Gnarosophia bellendenkerensis* varies in size, shape and colour throughout its range with some evidence of local geographic consistency in these characters (Fig. 3). Specimens from the Atherton Tbl. (*pterinus-castanea* forms, Fig. 3G-L) are smaller and darker in base colour than most due to the greater extent of the brown suffusion that largely obscures the subsutural yellow spiral band; specimens from the Gordonvale-Innisfail area (typical *bellendenkerensis*, Fig. 3A-C) tend to be very large with the two yellow spiral bands more prominent; and specimens from the Cardwell Ra. (*beddomae* form, Fig. 3D-F) are moderately large in size but with no brown suffusion separating the two yellow spiral bands, causing the shell to take on the bipartite colour pattern (yellow above, brown below) more commonly seen in *Hadra bipartita* and its allies.



FIG. 4. *Gnarosophia bellendenkerensis*, QMMO60242, Mt Lewis, col. R. Crookshanks.

There was, however, little discernible differentiation in reproductive anatomy and shell microsculpture between these forms. Hence, while the shell variation might indicate speciation trends in biogeographically isolated populations, there is insufficient morphological evidence to recognise more than one species.

Unfortunately there was no preserved material of the *Helix beddomae* form from the Cardwell Ra. available. This form of *G. bellendenkerensis* is of particular interest since it is an isolated southern population and has the most radical alteration in shell colour. A study of its soft parts may hold clues as to the nature of evolutionary trends in the species. Interestingly, the Cardwell Ra. is otherwise of special significance for land snails through the presence of the unusual helicarionid, *Theskelomensor creon* Solem, 1963.

DISCUSSION

Gnarosophia bellendenkerensis has peculiarities that make it both phylogenetically and biogeographically significant. On the basis of its genital structures and the presence of an eversible headwart, it belongs to the Camaeninae. Comparison of its reproductive anatomy with that of *Camaena cicatricosa* (Muller, 1774) (the type species of the type genus of the Camaenidae) from Hong Kong (Solem, 1992) shows that the basic plans are almost identical. *G. bellendenkerensis* has an epiphallic caecum developed about halfway along the epiphallus but otherwise has very similar structures (e.g. long convoluted free oviduct, clavate spermathecal head, Fig. 2A) to that of the Asian species. Perhaps more significant is the form of the penis interior. Both species have a rugosely sculptured verge with

terminal pore, and a pustulated upper chamber wall changing to a series of longitudinal ridges lower down and continuing into the atrium (Fig. 2B).

The striking similarity of the reproductive systems of these two species, coupled with the suggested origins of the eastern Australian Camaenidae as post-Miocene immigrants from the land masses to Australia's north (Bishop, 1981; Solem 1992; 1998) suggests that *G. bellendenkerensis* is a basal representative of the eastern Australian camaenid lineage that first colonised the Australian land mass. The lack of morphologic change in characters from those present in the extralimital species might be explained by evolution under basically stable environmental conditions since colonisation.

In spite of its wide occurrence in the Wet Tropics, it is nonetheless an environmentally restricted species in that it occurs chiefly above 400m. Confirmed recent records of lowland occurrences are few and are usually associated with riparian situations. There is a strong inference that these individuals were washed from higher altitudes and exist opportunistically in lower habitats. A similar altitudinal distribution was outlined for the helicarionid slug *Thularion semoni* von Martens, 1894 (Stanisic, 1993a) and also characterises members of the Pupinidae and Rhytididae (Stanisic, unpubl.). These examples are not unexpected and reflect the general altitudinal stratification of the Wet Tropics biota (Webb & Tracey, 1981; Keast, 1981). This phenomenon is usually particularly exemplified by the many cases of high mountain top endemics (Monteith, 1980; Stanisic, 1987; 1993b).

In the case of *G. bellendenkerensis* (and some other species of Wet Tropics land snails) a somewhat less marked altitudinal restriction is no less significant and infers the existence of a strong altitudinal biogeographic barrier. In fact the 400m contour represents a transition zone between the biota of the lowland humid complex mesophyll vine forests and that of the cooler upland and highland communities (Webb & Tracey, 1981). These latter communities were presumably more widespread at lower altitudes in the time-frame suggested for the first appearance of the camaenids in eastern Australia. With the drift of the continent into lower latitudes and a related altitudinal attenuation of biotic communities in the north, species were placed under considerable selective climatic pressure to adapt or retreat. In the case of *G. bellendenkerensis* populations appear to have followed the

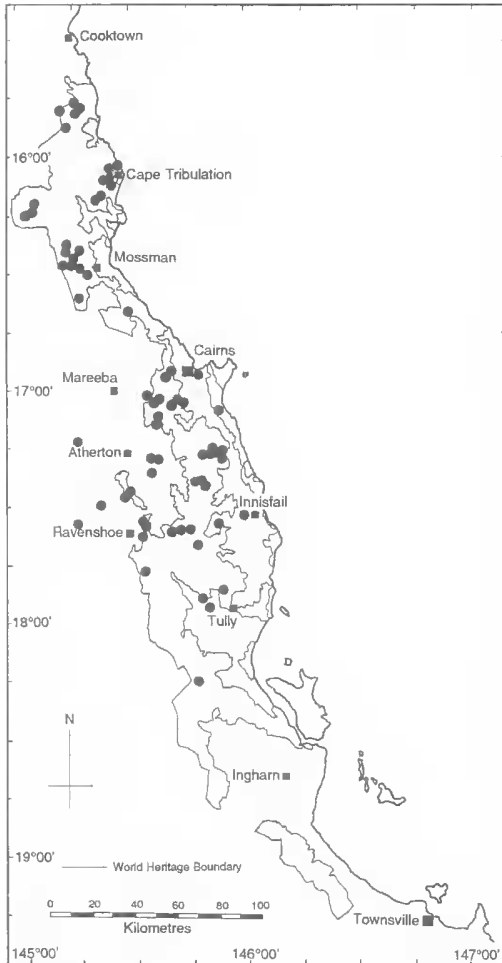


FIG. 5. Distribution map of *Gnarosiphia bellendenkerensis*.

upland retreat of the moist, cooler communities with little evidence of transition to the hotter, drier lowland forests, in spite of significant pressure to do so. This preference for the status quo in environmental conditions indicates a lack of adaptability but might also explain the lack of apparent morphological change in the species throughout its range.

Close study of the distribution of *G. bellendenkerensis* reveals that there is a series of discrete populations centred on the various rainforest blocks (refugia) in the Wet Tropics (Fig. 5). These isolates represent survivors of the Pleistocene restriction of mesic communities to very small upland and gully head refugia (Webb & Tracey,

1981; Nix, 1991). Though subsequent dispersal under more favourable climatic conditions may have led to expansion and even inter-block dispersal of populations, some climate-induced barriers between currently recognised blocks have persisted for a considerable period of time (e.g. Cardwell Ra.).

Hence, in spite of the lack of obvious morphological differences in these populations of *G. bellendenkerensis*, it could be expected that long-term isolation of populations has led to some level of genetic drift. Molecular studies will be needed to investigate the extent of these changes. The absence of sympatric congeners has meant that there has been little selective pressure for change from the base pattern in the terminal genitalia.

The relationship of *G. bellendenkerensis* to other hadroids is still problematic. The periostracal microsculpture bears some resemblance to that seen in some of the more southerly occurring hadroid species grouped in *Sphaerospira* by Smith (1992). These include *S. fraseri* (Griffith & Pidgeon, 1833) from southeastern Queensland and *S. informis* (Mousson, 1869) from mid-eastern Queensland and form part of a 'dark-animal' group (foot, mantle and tentacles grey to black) within *Sphaerospira* as opposed to species that display variously coloured animals (shades of mustard, pink, red, brown and orange on the foot, tentacles and neck) (Stanisic, 1996c). These latter species were previously placed in *Varohadra* Iredale, 1933 (+ *Figuladra* Iredale, 1933), *Bentosites* Iredale, 1933 and *Gnarosiphia* Iredale, 1933 by Iredale (1933, 1937). *Monteithosites* Stanisic, 1996 from Bakers Blue Mountain and Hanns Tbl. (Wet Tropics outliers) also has a coloured animal (red and brown). Stanisic (1996b,c) discusses this dichotomy in animal colours in some detail and suggests that these two groups are in fact biogeographically and phylogenetically distinct. [N.B. The type of *Varohadra* (= *Helix oconnellensis* Cox, 1871) is in fact a dark animal species and was associated with coloured animal species by Iredale (1937) without explanation. It will be shown elsewhere that this species is more closely related to *Sphaerospira* s.s.].

It is noteworthy that *S. fraseri* has a similar internally structured penis to *G. bellendenkerensis* (apical pustules and basal longitudinal pilasters) although a verge is absent in the former. A similar pattern is also present in other dark animal species e.g. *S. informis* (Mousson, 1869),

S. mortenseni (Iredale, 1929) and *S. blomfieldi* (Cox, 1864). In contrast many of the coloured animal forms have an extra pustular zone added to the base of the penial chamber and extensive pilaster modifications in the upper penial chamber (Stanisic, unpubl.). In that they correlate with basic differences in the periostracal microsculpture of the two species groups, these anatomical variations may be shown to be fundamental phylogenetic differences (rather than alterations related to sympatric species interactions) once additional studies are complete.

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LITERATURE CITED

- BISHOP, M.J. 1978a. A revision of the genus *Thersites* Pfeiffer (Pulmonata: Camaenidae). *Journal of the Malacological Society of Australia* 4: 9-21.
- 1978b. Anatomical notes on the Australian camaenid land snail *Sphaerospira fraseri* (Griffith & Pidgeon). *Journal of Molluscan Studies* 44: 200-208.
1981. The biogeography and evolution of Australian land snails. Pp. 924-954. In Keast, A. (ed.) *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- BRAZIER, J. 1875. Descriptions of ten new species of shells from the collection of Mr C. Coxen, of Brisbane, Queensland. *Proceedings of the Zoological Society of London* 1875: 31-34.
1878. Descriptions of seven new species of terrestrial and marine shells from Australia. *Proceedings of the Linnean Society of New South Wales* 3: 77-81.
- BURCH, I.B. 1976. Outline of the classification of Australian terrestrial molluscs (native and introduced). *Journal of the Malacological Society of Australia* 3: 127-156.
- CLENCI, W.J. & ARCHER, A.F. 1938. Some new Australian *Thersites*. *Journal of Conchology* 21: 20-24.
- COX, J. C. 1901. An alphabetical list of Australian land shells. (Frederick W. White: Sydney).
- FULTON, H. 1904. A critical list of the *Sphaerospira* (sic) species of *Thersites*. *Journal of Malacology* 11: 2-10.
- HEDLEY, C. 1890. Notes on Queensland land shells. *Proceedings of the Royal Society of Queensland* 6: 100-103.
- IREDALE, T. 1933. Systematic notes on Australian land shells. *Records of the Australian Museum* 19: 37-59.
1937. A basic list of the land Mollusca of Australia. Part II. *Australian Zoologist* 9: 1-39.
1938. A basic list of the land Mollusca of Australia. Part III. *Australian Zoologist* 9: 83-124.
- KEAST, A. 1981. Distribution patterns, regional biotas, and adaptations in the Australian biota: a synthesis. Pp. 1891-1998. In Keast, A. (ed.), *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- McMICHAEL, D.F. & IREDALE, T. 1959. The land and freshwater Mollusca of Australia. Pp. 224-245. In Keast, A., Crocker, R.L. & Christian, C.S. (eds) *Biogeography and Ecology in Australia*. (W. Junk: The Hague).
- MONTEITH, G.B. 1980. Relationships of the genera of Chinamyersiinae, with description of a relict species from mountains of north Queensland (Hemiptera: Heteroptera: Aradidae). *Pacific Insects* 21: 275-285.
- NIX, H.A. 1991. Biogeography: pattern and process. Pp. 11-39. In Nix, H.A. & Switzer, M.A. (eds) *Rainforest animals. Kowari 1*. (Australian National Parks and Wildlife Service: Canberra).
- ODJNER, N. 1917. Results of Dr E Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar* 52: 1-115.
- PILSBRY, H.A. 1890. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology. Conchological Section, Academy of Natural Sciences: Philadelphia Ser. 2, 6: 1-324.*
1894. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology. Conchological Section, Academy of Natural Sciences: Philadelphia Ser. 2, 9: 1-366.*
- SMITH, B.J. 1992. Non-marine Mollusca. Pp. 1-405. In Houston, W.W.K. (ed.) *Zoological Catalogue of Australia. Vol.8*. (Australian Government Publishing Service: Canberra).
- SMITH, B.J. & STANISIC, J. 1998. Pulmonata Introduction. Pp. 1037-1061. In Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) *Mollusca: the southern synthesis. Fauna of Australia. Vol. 5*. (CSIRO Publishing: Canberra).
- SOLEM, A. 1959. Systematics of the land and freshwater Mollusca of the new Hebrides. *Fieldiana Zoology* 43(1): 1-238.
1979. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum, Supplement No. 10: 5-142.*
1985. Simultaneous character convergence and divergence in Western Australian land snails. *Biological Journal of the Linnean Society* 24: 142-163.
1992. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo

- Island, Parts 1 & 2. Records of the South Australian Museum Monograph Series No. 2: 1-425.
1998. Family Camaenidae. Pp. 1112-1113. In Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) Mollusca: the southern synthesis. Fauna of Australia, Vol. 5. (CSIRO Publishing: Canberra).
- STANISIC, J. 1987. Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: a primitive genus from the high mountains of North Queensland (Mollusca: Pulmonata: Charopidae). Journal of the Malacological Society of Australia 8: 1-21.
- 1993a. The identity of *Helicarion semoni* Marten, 1894: a large semi-slug from the Wet Tropics, northeastern Queensland (Pulmonata: Helicarionidae). Memoirs of the Queensland Museum 34: 1-9.
- 1993b. *Danielleitona* gen. nov. From the Wet Tropics, northeastern Queensland (Pulmonata: Charopidae). Memoirs of the Queensland Museum 34: 11-20.
- 1996a. New land snails from boggomoss environments in the Dawson Valley, southeastern Queensland (Eupulmonata: Charopidae and Camaenidae). Memoirs of the Queensland Museum 39: 343-354.
- 1996b. A new camaenid land snail from the Wet Tropics Biogeographic Region, northeastern Queensland (Eupulmonata: Camaenidae). Memoirs of the Queensland Museum 39: 355-363.
- 1996c. The large camaenids of mideastern Queensland. Australasian Shell News 92: 1-2.
1998. *Temporena* Iredale, 1933 unravelled. Memoirs of the Queensland Museum 42: 604.
- STANISIC, J., EDDIE, C., HILL, A. & POTTER, D. 1994. Preliminary report on the distribution of land snails occurring within the Wet Tropics area. 18pp, 222 maps. Report to the Wet Tropics Management Authority. (Queensland Museum: Brisbane).
- WEBB, L.J. & TRACEY, J.G. 1981. Australian rainforests: patterns and change. Pp. 605-694. In Keast, A. (ed.) Ecological biogeography of Australia. (Dr W. Junk: The Hague).
- ZILCH, A. 1959. Euthyneura. In Schindewolf, O.H. (ed.) Handbuch der Paläozoologie. Borntraeger: Berlin: Berlin-Zehlendorf. Bd 6.11.2. xii 834 pp.